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A new species of the endemic genus *Hemicyrthus* Reiche (Coleoptera: Scarabaeidae: Dynastinae) from New Caledonia, with a revised key

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Abstract

Hemicyrthus blaffarti new species (Coleoptera: Scarabaeidae: Dynastinae) from the Parc Provincial de la Rivière Bleue in southern New Caledonia is described. It differs from the most similar species, *H. elongatus*, by the completely and sharply margined pronotal base, the presence of elytral micropunctures, shorter apical setae of the mesotibiae and metatibiae, and a different shape of the parameres. For the first time, a sexually dimorphic character is described in this genus: the median emargination of the last sternite has a developed margin in males, but not in females. A revised key for all *Hemicyrthus* species is given. *Hemicyrthus* as a genus of short-range endemics, and its biogeographical relationships are briefly discussed.

Key words: rhinoceros beetle, short-range endemics, Madagascar, Hexodontini, Oryctoderini

Introduction

New Caledonia is one of the 25 biodiversity hotspots on earth as identified by Myers *et al.* (2000). A high proportion of endemic taxa, which have undergone extensive radiation with species inhabiting very small areas (short-range endemics), is a common pattern of the New Caledonian flora and fauna (Grandcolas *et al.* 2008). This pattern is exemplified by *Hemicyrthus* Reiche in Montrouzier, 1860, a genus of rhinoceros beetles (Coleoptera: Scarabaeidae: Dynastinae) comprising six described species, most of which are known from singletons or only a few specimens (Dechambre 1982; Paulian 1991). During the last decade, one of us (J.T.) collected four males and six females, all dead, of a new *Hemicyrthus* species in the rainforest of the Parc Provincial de la Rivière Bleue, in the south of the island (Fig. 1). This species is here described and included in a revised key for all *Hemicyrthus* species.

Study area

Parc Provincial de la Rivière Bleue (22°03′–12′S, 166°33′–46′E; Fig. 1) is a 90-km² reserve located in southern New Caledonia. It was created in 1980, after forest exploitation of kauri (*Agathis lanceolata* Lindley ex Warburg, Araucariaceae) ceased. The region comprises part of the southern massif, a large expanse of ultramafic (ultrabasic) rock. Most soils in the area are highly weathered and poor in nutrients but with high heavy metal contents (Jaffré & Veillon 1991). In the valley of the Rivière Bleue, richer alluvial soils support lowland rainforest with a dense canopy and a height of roughly 20–25 m (Jaffré & Veillon 1991). The mean annual temperature in the forest is 18°C, and the mean annual rainfall in the Rivière Bleue valley is 3,181 mm, which makes it one of the wettest lowland areas in New Caledonia (Bonnet de Larbogne *et al.* 1991). There are three seasons in New Caledonia: the cool/rainy season (May–August), the warm/dry season (September–December) and the hot/rainy season (January–April). Main potential threats to Scarabaeidae in this area consist of little fire ants, *Wasmannia auropunctata*

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(Roger, 1863) (Hymenoptera: Formicidae), introduced accidentally to the study area in about 1997 (Le Breton *et al.* 2003); and introduced black rats, *Rattus rattus* (Linnaeus, 1758) (Rodentia: Muridae), which are common in the Rivière Bleue valley forest (Rouys & Theuerkauf 2003).





FIGURE 1. Parc Provincial de la Rivière Bleue in southern New Caledonia. A: Close to the type locality (Fig. 1C), after heavy rainfall. B: Parc Provincial de la Rivière Bleue, typical rainforest in the valley (photograph: Thorsten Müller). C: Refuge des Scientifiques, type locality of *Hemicyrthus blaffarti*. House in which the holotype was found is in the upper left corner.

Repositories

BMNH CXMNC The Natural History Museum, Department of Life Sciences, London, United Kingdom.

Collection de Référence des Invertébrés Terrestres de Nouvelle-Calédonie - Xavier Montrouzier. Institut Agronomique néo-Calédonien, Station de Recherche Agronomique de Pocquereux, La Foa, New Caledonia.

DMNS Denver Museum of Nature & Science, Department of Zoology, Denver, Colorado, United States of

America.

MNHN Muséum national d'Histoire naturelle, Entomologie, Paris, France.

Hemicyrthus blaffarti Krell, new species

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Types. Holotype (male; Fig. 2): NEW CALEDONIA, Parc Provincial de la Rivière Bleue, Refuge des Scientifiques, 166°38′42″ E, 22°6′5″ S, alt. 190 m, rainforest, leg. J. Theuerkauf 15.xii.2006, dead [flagella of antennae missing; terminal two right protarsomeres missing, terminal four left metatarsomeres missing]; deposited in MNHN, Paris.

Paratypes. All from NEW CALEDONIA, Parc Provincial de la Rivière Bleue. 1 ♀: Refuge de la Rivière Bleue, 166°38′19" E, 22°5′51" S, 200 m, rainforest road, leg. J. Theuerkauf 22.viii.2012, dead [disc of elytra dented and cracked, left mesotarsus missing], DMNS ZE.46269. 1 ♀: Pont Germain, 166°39′27″ E, 22°6′3″ S, 180 m, road in riverside forest, leg. J. Theuerkauf 8.vi.2011, dead [antennae missing, terminal four right protarsomeres and both terminal four metatarsomeres missing], DMNS ZE.46270. 1 \circlearrowleft : Pont Germain, 166°39′20″ E, 22°5'5" S, 180 m, rainforest road, leg. J. Theuerkauf 29.xii.2012, dead [mouthparts and left antenna, left metatarsus and three terminal mesotarsomeres missing; left anterior margin of clypeus damaged], DMNS ZE.46271. 1 ♀: Grand Kaori, 166°40′38" E, 22°5′50" S, 180 m, rainforest track, leg. J. Theuerkauf 10.x.2006, dead [left protarsi and metatarsi missing], DMNS ZE.46272. 1 \(\times\): 166°40′0″ E, 22°5′59″ S, 180 m, rainforest road, leg. J. Theuerkauf 24.ix.2006, dead [terminal two right protarsomeres missing], DMNS ZE.60956 (Fig. 3). 1 🗜: 166°38'25"-40'38" E, 22°5'50"-6'5" S, 180-200 m, road, leg. J. Theuerkauf 2003/2004, dead [right front leg, terminal two left protarsomeres, left mesotarsus, terminal two right mesotarsomeres, terminal four left metatarsomeres, terminal three right metatarsomeres and terminal seven right antennomeres missing], CXMNC. 1 ♂: 166°38′25″–40′38″ E, 22°5′50″–6′5″ S, 180–200 m, road, leg. J. Theuerkauf 15.ii.2006, dead [all tarsomeres missing apart from first on right front leg and three on right middle leg; some glued on card; antennae and majority of mouthparts missing; cuticular surface matte due to weathering], DMNS ZE.46273. 1 \(\text{ : } 166\circ 38'25''-40'38''\) E, 22°5′50"-6′5" S, 180-200 m, road, leg. J. Theuerkauf 18.x.2006, dead [crushed; terminal four right protarsomeres and both terminal four metatarsomeres missing], DMNS ZE.46274. 1 3: 166°38′25″–40′38″ E, 22°5′50″–6′5″ S, 180-200 m, road, leg. J. Theuerkauf 15.x.2007, dead [right antenna and left flagellum missing; both terminal four protarsomeres missing, terminal three left mesotarsomeres missing, four terminal right mesotarsomeres missing, hole in propygidium, left elytral tip damaged], CXMNC.

Diagnosis. Dorsally glabrous *Hemicyrthus* with pronotum completely margined laterally, but without margin or strong oblong punctures at the base; scutellum punctate, longer than wide elytra without keels; apical mesotibial and metatibial setae, short, blunt.

Description. \circlearrowleft (**Fig. 2**). *Dimensions*. Body length: 21.1–22.1 mm (holotype: 21.1 mm; arithmetic mean $\overline{\chi}_{n=4}$ = 21.6 mm; range of variation R = 1.0 mm = 4.6 %). Maximum width of pronotum: 9.3–10.4 mm (holotype: 9.8 mm; $\overline{\chi}_{n=4}$ = 9.9 mm; R = 1.1 mm = 11.1 %). Maximum width of elytra: 11.6–13.1 mm (holotype: 12.9 mm; $\overline{\chi}_{n=4}$ = 12.6 mm; R = 1.5 mm = 11.9 %).

Colour. Blackish brown to black.

Microsculpture. Areas between the dense, fine punctures flat, aciculate and covered by dense, sometimes superficial micropunctures.

Setation. Upper side, prosternum, metasternum, pygidium and sternites glabrous. Mesosternum with medium dense, short, brown setae.

Epicranium. Sides converging to clypeus, either straight or slightly convex. Clypeus with blunt lateral lobes, concave in-between. Distance between clypeal lobes about a quarter of epicranial width. Epicranial surface slightly convex, without tubercles or ridges, but slightly bulged in the middle of the anterior half. Frontoclypeal suture complete, forming a fine, impressed line. Area anterior to frontal suture with dense, fine punctation; posterior to suture without or with barely visible, superficial punctation except laterally where some superficial fine punctures are more distinct; rarely with clearly visible, but still superficial punctation in median area behind suture [*e.g.*, in holotype].

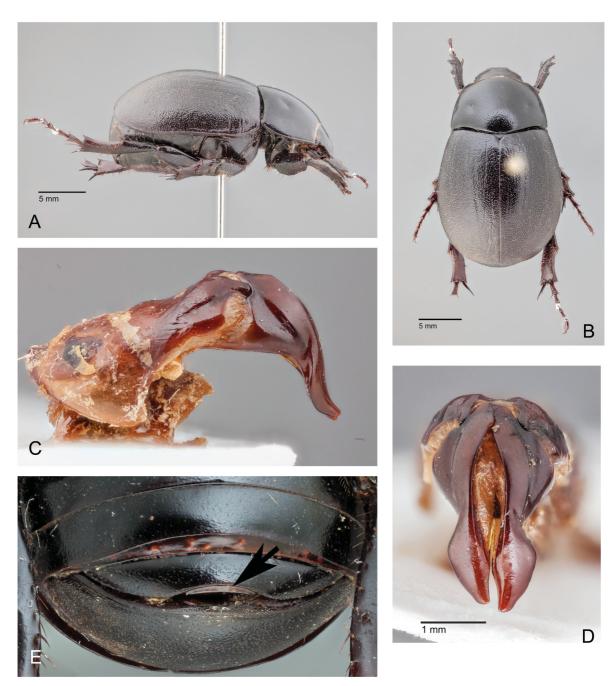


FIGURE 2. *Hemicyrthus blaffarti* new species male, holotype (MNHN). A: lateral. B: dorsal. C: aedeagus lateral. D: parameres dorsal. E: apex of abdomen. Arrow indicating the sexually dimorphic emargination of the last sternite.

Ocular canthus. Lateral lobes in front of eyes short, but protruding and convex (if not worn), without setae. The lobes barely extend into an ocular canthus, but notch the eyes.

Mandibles. External margin slightly bilobed; tip blunt; dorsally smooth and glabrous; ventrally with punctures and setae.

Labium. Broad, moderately tapering anteriorly; discally bulged with sparse, long setae and large punctures. Apically concave. Anterolateral angles flat triangular, slightly convex to almost straight in-between.

Antennae. With 10 antennomeres, without signs of fusion of antennomeres. Terminal antennomere inserts distant from the base of the penultimate antennomere. Penultimate antennomere inserts distant from the base of eighth antennomere. Scapus and club with long and finer setae, respectively.

Pronotum. Weakly convex, without tubercles or other sculpture; with fine, dense punctation and sparse micropunctures; and with a weak lateral impression on each side (in the holotype only, also with a laterodiscal

impression on each side that is probably teratological). Lateral margins convex. Anterior angles acute but not sharp. Posterior angles obtuse. Only lateral margins with border. Basal margin with sparse, fine, superficial punctures, without stripe-like longitudinal punctures.







FIGURE 3. Hemicyrthus blaffarti new species, female, paratype DMNS ZE.60956. A: lateral. B: dorsal. C: apex of abdomen.

Prosternal process. Approximately cylindrical, dorsoventrally oriented, ventrally extending as far as the coxae protrude, with blunt tip bearing long setae.

Tibiae. Protibia tridentate, with sharp apical spur inserted at a level with the base of the middle external denticle and reaching the end of the second tarsomere. Mesotibiae and metatibiae with the anteapical transversal ridge and apex bearing short, blunt, flattened setae, which are up to 3 times as long as broad. Setal punctures notch tibial apex and transversal ridge.

Scutellum. Triangular, about 1.7x as broad as long, with straight sides and sharp tip; with few round or oval punctures the size of the elytral punctures.

Elytra. Fused. Glabrous and smooth, without ridges, but with 4–6 rudimentary striae, mainly on the anterior half. Anterior half as shiny as pronotum; slightly dull towards the apex. Punctures fine and dense, but slightly larger and deeper than on pronotum; in posterior half transversally wrinkled. Micropunctures sometimes shallow, but visible.

Alae. Lacking.

Pygidium. Propygidium and pygidium fused with distinct suture; fine, but strongly wrinkled at the base, so that the punctures are only visible on the apical three quarters or less than the apical half of the pygidium, where the surface is smooth and shiny.

Last sternite with broad median emargination, margin of emargination dorsally developed (this being the noticeable sexual dimorphism in this species and probably the genus; Fig. 2E).

Aedeagus. Fig. 2C, D.

 \mathcal{L} (Fig. 3). No major sexual dimorphism. Characters as in \mathcal{L} with following exceptions:

Dimensions. Body length: 19.1–21.5 mm ($\frac{1}{X_{n=5}}$ = 20.7 mm; range of variation R = 2.4 mm = 11.6 %). Maximum width of pronotum: 9.0–10.0 mm ($\frac{1}{X_{n=5}}$ = 9.5 mm; R = 1.0 mm = 10.5 %). Maximum width of elytra: 11.6–12.6 mm ($\frac{1}{X_{n=5}}$ = 12.2 mm; R = 1.0 mm = 8.2 %).

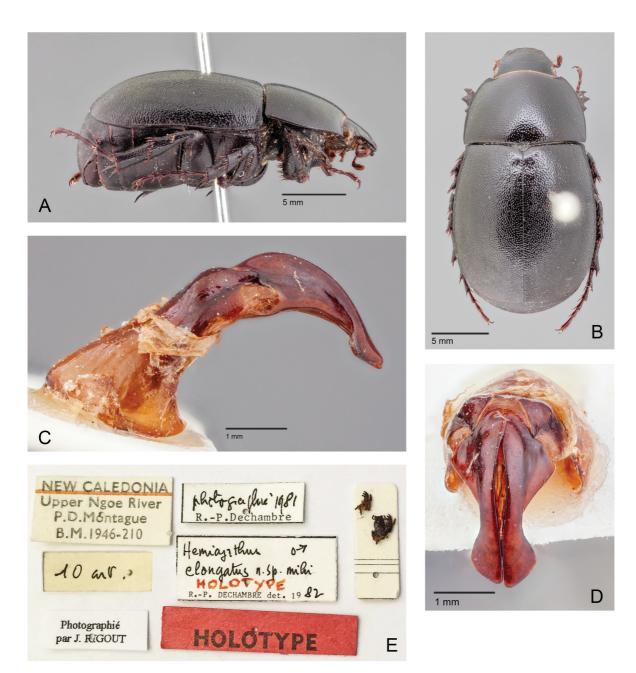


FIGURE 4. *Hemicyrthus elongatus* Dechambre, male, holotype (BMNH). A: lateral. B: dorsal. C: aedeagus lateral. D: parameres dorsal. E: labels and dissected mouthparts.

Last sternite with narrower median emargination, but margin not developed (Fig. 3C).

Distribution. New Caledonia, Province Sud, Parc Provincial de la Rivière Bleue (see Bonnet de Larbogne *et al.* 1991). Type locality: Refuge des Scientifiques, 166°38′42″E, 22°6′5″S (Fig. 1C).

Etymology. Named in honour of Henri Blaffart (1965–2008), a Belgian conservationist who worked in New Caledonia for Conservation International on projects with strong community involvement (McKenna *et al.* 2006; Saunders *et al.* 2007). He was a founding member of the association Dayu Biik, which is involved in the conservation of the Mt Panié. He was killed in an accident on the Tiendanite River in the Northern Province on 21 March 2008 while working on the Mt Panié conservation project. For a photograph of Henry Blaffart see McKenna *et al.* (2006: 126).

Comparison with similar Hemicyrthus species

Three described *Hemicyrthus* species resemble the new species morphologically, namely *H. chazeaui* Dechambre, 1982 from Mont Do (Province Sud), *H. elongatus* Dechambre, 1982 from the Upper Ngoe River (Province Sud) and *H. serresii* (Montrouzier, 1860) from the island of Belep in the north (map: Fig. 5). The former two species have the most similar aedeagal shape with a laterally extended, triangular tip of the parameres and they occur geographically nearest to *H. blaffarti* compared to all other *Hemicyrthus* species.

The geographically more distant *H. serresii* can be easily distinguished from the other three species in this group by its margined pronotal base and the tapering, not triangularly extended parameral tips. The micropunctures on its elytral disk are reduced, but sparsely present on the sides and apex.

Hemicyrthus chazeaui, of which we could examine the holotype only, has no micropunctures on the elytra, whereas in *H. blaffarti* they are often weak but always visible. The sharp, longitudinal elongate punctures on the basal margin of the pronotum of *H. chazeaui* are lacking in *H. blaffarti*. In *H. chazeaui*, the elytral punctures are smaller, less impressed than in *H. blaffarti*, apically barely confluent, but forming flat transversal wrinkles with the rasp-like punctures still being separated. The shallow, rugose microsculpture of the propygidium and pygidium in *H. chazeaui* leaves the sparse punctures visible all over except for the lateral angles of the pygidium, where the microsculpture becomes stronger; whereas in *H. blaffarti*, the propygidium and basal area of the pygidium are strongly wrinkled. Dechambre's (1982: fig. 1) drawing of the aedeagus of *H. chazeaui* is largely correct, but the tips of the parameres are more broadly rounded. For the shape of the parameres in *H. blaffarti*, see Fig. 2C, D.

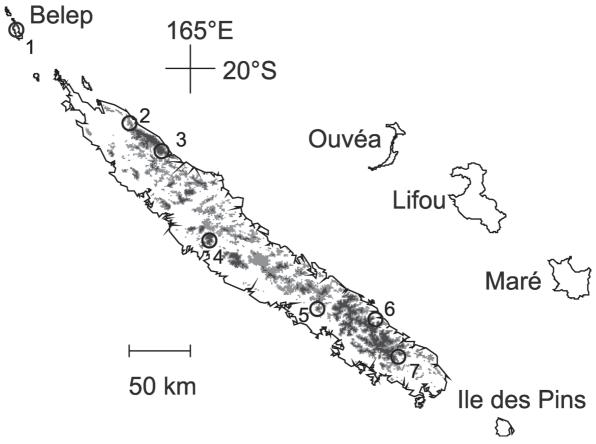


FIGURE 5. Published collecting localities of *Hemicyrthus* species (Dechambre 1982; Paulian 1991; Théry 2008; present study). 1. *Hemicyrthus serresii* (Montrouzier, 1860), Iles Belep; 2. *Hemicyrthus villersi* (Montrouzier, 1860), Mont Mandjélia; 3. *Hemicyrthus villersi* (Montrouzier, 1860), Mont Panié; 4. *Hemicyrthus costatus* Dechambre, 1982, Mont Boulinda; 5. *Hemicyrthus chazeaui* Dechambre, 1982 and *Hemicyrthus gutierrezi* Dechambre, 1982, Mont Do; 6. *Hemicyrthus elongatus* Dechambre, 1982, Upper Ngoe River; 7. *Hemicyrthus blaffarti* new species, Parc Provincial de la Rivière Bleue. Dark grey area (elevation 700–1628 m), light grey area (elevation 300–700 m), white area (elevation under 300 m). *Hemicyrthus reichei* Dechambre, 1982, is not indicated in this map because it was described from a historical specimen labelled "N.Caled." without further detail.

Hemicyrthus elongatus (Fig. 4) is the most geographically and morphologically close species to *H. blaffarti*. It is only known from the holotype (Dechambre 1982; Théry 2008). All observed differences between the two species are in the key below.

Phenology

Although all specimens were collected dead, the fair or good condition of the specimens indicates that they died within a couple of hours or few days of when they were found. Only the specimen collected in February shows signs of longer exposure. While we worked in the field throughout the year, the specimens were found in February (1), June (1), August (1), September (1), October (3) and December (2). We thus found most dead adult individuals during the cool/rainy season and especially the warm/dry season.

Key to species

Based on Dechambre (1982), extended and revised.

1	Apical half of elytra with short, yellow setae; clypeus very indistinctly emarginate
-	Dorsal surface completely glabrous; clypeus distinctly emarginate
2	Elytra with 3 distinct yet blunt keels; pronotum smooth (punctures expressed as flat shiny dots in the dull microsculpture) H. costatus Dechambre
-	Elytra without keels (in <i>H. reichei</i> and <i>H. gutierrezi</i> with 3 shallowly impressed longitudinal stripes; similar in <i>H. serresii</i>); pronotum with impressed punctures
3	Elytra shorter than combined width
-	Elytra longer than combined width
4	Base of pronotum margined (except at the middle)
-	Base of pronotum not margined
5	Base of pronotum finely margined
-	Base of pronotum not margined, except at the angles
6	Scutellum punctate; antennae with 10 antennomeres ¹ . Basal margin of pronotum without elongate punctures
	Scutellum mainly smooth (only 2 small punctures at the middle); antennae with 9 antennomeres. Basal margin of pronotum with sharp, longitudinal, elongate punctures
7	Pronotum laterally completely and sharply marginated. Elytral microsculpture: areas between punctures flat, with dense micro-
,	punctures. Apical setae of mesotibiae and metatibiae up to 3 times as long as broad. Aedeagus: Fig. 2C, D
-	Only posterior half of sides of pronotum margined, impressed line of margin interrupted and faded before reaching the posterior
	rior angles. Elytral microsculpture leathery rugulose or granulate, areas between punctures convex, without micropunctures.
	Apical setae of mesotibiae and metatibia up to 7 times as long as broad. Aedeagus: Fig. 4C, D
	H. elongatus Dechambre (Fig. 4)

Hemicyrthus, a genus of short-range endemics

All seven *Hemicyrthus* species are known from few specimens, sometimes only from the holotype (Dechambre 1982; Paulian 1991; Théry 2008). They all are known from either single locations or small areas (Fig. 5). The species with the widest known range is *H. villiersi* from Mont Mandjelia to Mont Panié, which are just over 30 km apart and are connected by a continuous mountain forest. The next largest range is that of *H. blaffarti*, with Refuge de la Rivière Bleue in the east and Grand Kaori in the west of its known range being just over 4 km apart. The other species are known from one locality only, with no available spatial data about the collecting area.

Short-range endemism is common in New Caledonia with numerous examples in, *e.g.*, reptiles, plants and insects (Murienne *et al.* 2008), and is promoted by low dispersal capability and low ecological tolerance (Ponder & Colgan 2002). The ecological requirements of *Hemicyrthus* species are unknown, but the flightlessness and substantial size of the *Hemicyrthus* species greatly restrict their active and passive dispersal abilities.

^{1.} Since the number of antennomeres can vary intraspecifically in Dynastinae and other groups of Scarabaeidae (Krell 1992), this diagnostic character is tentative, considering that only twelve specimens are known of the three species.

A New Caledonia-Madagascar connection?

The systematic placement of the genus *Hemicyrthus* has a controversial history that is yet to be resolved. It has been considered as belonging to the otherwise exclusively Malagasy tribe Hexodontini (Dechambre 1982; Paulian 1991) because the first *Hemicyrthus* species was described by Montrouzier (1860) as *Hexodon villersi*. For this tribe Paulian (1961: 154) used, probably erroneously, the name "Hemicyrtini" (correct: Hemicyrthini), and included *Hexodon* and *Hemicyrtus* (correct: *Hemicyrthus*). Then, Endrődi (1976) transferred *Hemicyrthus* to the Pacific-Australian tribe Oryctoderini and maintained this opinion in his world monograph of Dynastinae (Endrődi 1985). This was disputed by Dechambre (1986) who clarified that the insertion of the last antennomere distant from the base of the penultimate antennomere and the reduced ocular canthus are presumed tribal apomorphies for Hexodontini and indicate the placement of *Hemicyrthus* in this tribe as originally thought. However, the genus is still listed under Oryctoderini by Krajcik (2005) in his recent catalogue of Dynastinae. Lacking autapomorphies, the tribe Oryctoderini is poorly diagnosed and its taxonomic status and phylogenetic position require revision (Jameson & Ratcliffe 2009).

New Caledonia had long been thought to have preserved some old Gondwanan lineages, but given the tectonic history of Gondwana, a sister-group relationship between a genus on Madagascar (*Hexodon*) and one on New Caledonia (*Hemicyrthus*) would be unexpected (see Sanmartín & Ronquist 2004). More recent evidence indicates a submergence of New Caledonia between the Cretaceous and Eocene (Pelletier 2007) and the subsequent recolonisation of the island since the Eocene (Espeland & Murienne 2011, Swenson *et al.* 2014), which makes this sister-group relationship even less likely. To our knowledge, the only comparable case is the angiosperm genus *Acridocarpus* Guillemin & Perrottet (Malpighiaceae) with a single New Caledonian species being nested in a clade with two Malagasy species (Davis *et al.* 2002). Transoceanic dispersal has been suggested to be the likely mechanism behind this relationship, but for large beetles oceanic dispersal seems to be less plausible than for seeds.

How could such a relationship in the Hexodontini be explained? The shape of the antennal club and the reduced ocular canthus might be convergent in *Hemicyrthus* and *Hexodon*. If *Hemicyrthus* does not belong to the Hexodontini then a biogeographical connection to Madagascar does not exist. If those characters are synapomorphies, however, then *Hemicyrthus* and *Hexodon* are Gondwanan relicts with the Hexodontini having become extinct in India, Australia and New Zealand. In such a scenario, the stem species of *Hemicyrthus* would have colonised New Caledonia from some less distant land in or after the Eocene.

Since *Hemicyrthus blaffarti* belongs to the more slender species of the genus that have a body shape distinct from the broad-bodied *Hexodon*, this new species does not appear to provide any further morphological evidence for the phylogenetic relationship of the two genera. We will likely have to wait for molecular evidence to solve this problem.

Acknowledgements

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References cited

Bonnet de Labrogne, L., Chazeau, J., Tillier, A. & Tillier, S. (1991) Milieux naturels néo-calédoniens : la Réserve de la Rivière Bleue. *Mémoires du Muséum National d'Histoire Naturelle, Paris (A)*, 149, 9–17.

Davis, C.C., Bell, C.D., Fritsch, P.W. & Mathews, S. (2002) Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): implications for Tertiary tropical floras and Afroasian biogeography. *Evolution*, 56, 2395–2405.

- http://dx.doi.org/10.1111/j.0014-3820.2002.tb00165.x
- Dechambre, R.-P. (1982) Contribution à l'étude phylogénétique des Hexodontini (Coleoptera, Dynastidae). Étude systématique préliminaire du genre *Hemicyrthus* Reiche. *Revue Française d'Entomologie*, N.S., 4, 101–107.
- Dechambre, R.-P. (1986) Insectes Coléoptères Dynastidae. Faune de Madagascar, 65, 1-215.
- Endrődi, S. (1976) Monographie der Dynastinae, 7. Tribus: Hexodontini. *Annales Historico-Naturales Musei Nationalis Hungarici*, 68, 141–153.
- Endrődi, S. (1985) The Dynastinae of the World. Akadémiai Kiadó, Budapest, 800 pp., 46 pls.
- Espeland, M. & Murienne, J. (2011) Diversity dynamics in New Caledonia: towards the end of the museum model? *BMC Evolutionary Biology*, 11, 254.
 - http://dx.doi.org/10.1186/1471-2148-11-254
- Grandcolas, P., Murienne, J., Robbilard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E. & Deharveng, L. (2008) New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society B*, 363, 3309–3317. http://dx.doi.org/10.1098/rstb.2008.0122
- Jaffré, T. & Veillon, J.-M. (1991) Etude floristique et structurale de deux forêts dense humides sur roches ultrabasiques en Nouvelle-Calédonie. Bulletin du Muséum National d'Histoire Naturelle, Série 4e, 12, Section B, Adansonia, 3–4, 243–273
- Jameson, M.L. & Ratcliffe, B.C. (2009) Revision of the genus *Chalcasthenes* Arrow (Coleoptera: Scarabaeidae: Dynastinae: Oryctoderini) from the Solomon Islands. *Australian Journal of Entomology*, 48, 149–163. http://dx.doi.org/10.1111/j.1440-6055.2009.00699.x
- Krajcik, M. (2005) Dynastinae of the world checklist (Coleoptera: Scarabaeidae: Dynastinae). *Animma.x Supplement*, 2, 1–122. Krell, F.-T. (1992) Verschmelzung von Antennomeren (Symphysocerie) als Regelfall bei *Temnorhynchus repandus* Burmeister, 1847, sowie phylogenetische, taxonomische, faunistische und nomenklaturische Anmerkungen zu diversen Taxa dieser Gattung (Coleoptera. Scarabaeoidea, Melolonthidae, Dynastinae, Pentodontini). *Deutsche Entomologische Zeitschrift*, N.F., 39, 295–367.
- Le Breton, J., Chazeau, J. & Jourdan, H. (2003) Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology*, 28, 204–209. http://dx.doi.org/10.1046/j.1442-9993.2003.01266.x
- McKenna, S.A., Baillon, N., Blaffart, H. & Abrusci, G. (2006) Une évaluation rapide de la biodiversité marine des récifs coralliens du Mont Panié, Province Nord, Nouvelle Calédonie. *Bulletin PER d'Evaluation Biologique*, 42, 1–126.
- Montrouzier, [J.X.H.] (1860) Essai sur la faune entomologique de la Nouvelle-Calédonie (Balade) et des îles des Pins, Art, Lifu, etc. *Annales de la Société Entomologique de France*, Series 3, 8, 229–308, pl. 7.
- Murienne, J., Pellens, R. & Grandcolas, P. (2008) Short-range endemism in New Caledonia. New species and distribution of the genus *Lauraesilpha* Grandcolas, 1997 (Insecta, Dictypotera, Blattidae, Tryonicinae). *Mémoires du Muséum National d'Histoire Naturelle*, 197, 261–271.
- Myers, M., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. da & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. http://dx.doi.org/10.1038/35002501
- Paulian, R. (1961) La zoogéographie de Madagascar et des îles voisines. Faune de Madagascar, 13, 1-485.
- Paulian, R. (1991) Les Coléoptères Scarabaeoidea de Nouvelle-Calédonie (Faune Tropicale 29). Orstom, Paris, 166 pp.
- Pelletier, B. (2007) Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity. *In*: Payri, C.E. & Richer de Forges, B. (Eds.), *Compendium of Marine Species of New Caledonia. (Documents Scientifiques et Techniques, II (7), 2nd Edition)*. Institute de Recherche pour le Développement, Centre de Nouméa, New Caledonia, pp. 19–32.
- Ponder, W.F. & Colgan, D.J. (2002) What makes a narrow-range taxon? Insights from Australian freshwater snails. *Invertebrate Systematics*, 16, 571–582. http://dx.doi.org/10.1071/IT01043
- Rouys, S. & Theuerkauf, J. (2003) Factors determining the distribution of introduced mammals in nature reserves of the southern province, New Caledonia. *Wildlife Research*, 30, 187–191. http://dx.doi.org/10.1071/WR01116
- Sanmartín, I. & Ronquist, F. (2004) Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology*, 53, 216–243. http://dx.doi.org/10.1080/10635150490423430
- Saunders, A., Blaffart, H., Morley, C., Kuruyawa, J., Masibalavu, V. & Seniloli, E. (2007) A "community" approach to invasive species management: some Pacific case studies. *In:* Witmer, G.W., Pitt, W.C. & Fagerstone, K.A. (Eds.), *Managing Vertebrate Invasive Species: Proceedings of an International Symposium.* United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Service, National Wildlife Research Center, Fort Collins, Colorado, pp. 29–33.
- Swenson, U., Nylinder, S. & Munzinger, J. (2014) Sapotaceae biogeography supports New Caledonia being an old Darwinian island. *Journal of Biogeography*, 41, 797–809. http://dx.doi.org/10.1111/jbi.12246
- Théry, T. (2008) Nouvelles captures concernant le genre *Hemicyrthus* Reiche, 1860 (Col., Dynastidae, Hexodontini). *Bulletin de la Société Entomologique de France*, 113, 341–342.